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Numerical assessment in the wild: Insights from social carnivores

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Summary

Playback experiments have proven to be a useful tool to investigate the extent to which wild animals understand numerical concepts and the factors that play into their decisions to respond to different numbers of vocalizing conspecifics. In particular, playback experiments have broadened our understanding of the cognitive abilities of historically understudied species that are challenging to test in the traditional laboratory, such as members of the Order Carnivora. Additionally, playback experiments allow us to assess the importance of numerical information versus other ecologically important variables when animals are making adaptive decisions in their natural habitats. Here, we begin by reviewing what we know about quantity discrimination in carnivores from studies conducted in captivity. We then review a series of playback experiments conducted with wild social carnivores, including African lions, spotted hyenas, and wolves, which demonstrate that these animals can assess the number of conspecifics calling and respond based on numerical advantage. We discuss how the wild studies compliment those conducted in captivity and allow us to gain insights into why wild animals may not always respond based solely on differences in quantity. We then consider the key role that individual discrimination and cross-modal recognition play in the

ability of animals to assess the number of conspecifics vocalizing nearby. Finally, we explore new directions for future research in this area, highlighting in particular the need for further work on the cognitive basis of numerical assessment skills and experimental paradigms that can be effective in both captive and wild settings.

Introduction

Numbers play an essential role in everyday life for most, if not all, animals. The ability to assess quantitative differences enables individuals from prey species, such as guppies, to reduce predation risk by preferentially joining larger social groups [1–6]. Likewise, predators benefit from the ability to discriminate quantities when selecting foraging patches and when choosing which size of prey to hunt, which can change depending on the number of partners in a hunting party [7–10]. Individuals can also increase their chance of reproducing successfully by selecting a group with a more advantageous sex ratio [11,12] and parents can employ numerical abilities to enhance the survival of their offspring. For example, American coots reduce brood parasitism by keeping track of the number of eggs they have laid and rejecting any additional eggs that appear in their nest [13]. Social species utilize a number sense when assessing competitive advantage during intergroup conflicts [14–17] and in the context of filial imprinting. For example, recently hatched domestic chicks utilize numerical abilities to spontaneously associate with the more numerous group of social companions [18]. Thus, it seems clear that a keen sense of number and the ability to discriminate between quantities aids in the successful survival and reproduction of most animals.

Given the importance of numerical abilities for most animals, it is not surprising that numerical cognition has been the subject of intense study in the fields of comparative cognition and cognitive neuroscience. Researchers in these fields have found that the ability to discriminate between different numbers of objects appears to be a foundational cognitive ability and have documented this ability in numerous species across the Animal Kingdom. For example, quantity

discrimination has been demonstrated experimentally in several species of fish [5,11,19–21], amphibians [8,22,23], birds [18,24–35], mammals [9,36–41], primates [42–45], human infants [46–49] and even some invertebrates [50–52]. The only study testing quantity discrimination in a reptile found that although ruin lizards (*Podarcis sicula*) do spontaneously select the larger quantity of food, they do not spontaneously select the option with a higher number of food items [53]. However, the vast majority of the literature in this field suggests that animals likely share an ability to assess number.

Relative Quantity Judgements in Captive Carnivores

Within the Order Carnivora, there are data showing quantity discrimination by members of the Felidae [14,54,55], Canidae [56–60], Ursidae [61], Procyonidae [62], Otariidae [63], and Hyaenidae [15] families. Most of these studies have been conducted with captive animals and have asked test subjects to discriminate between different quantities of food [54,56,57]. For example, Ward and Smuts [56] inquired whether domesticated dogs could choose the larger quantity of food in two experiments. In the first experiment, 29 dogs were presented with two different quantities of food in a forced-choice task. The food choices were presented simultaneously in eight different combinations and were visually available when the dogs made their selection. The dogs were able to select the larger versus smaller quantity of food, and their performance declined when the numerical distance between the two quantities decreased as well as when the ratio between the two quantities increased. Thus, the performance of domestic dogs followed Weber's law, which states that the size of the just noticeable difference between two stimuli depends on the ratio between the two magnitudes rather than the absolute difference [64]. Therefore, the comparison becomes more difficult as the numerical distance between two quantities becomes smaller and as the ratio of the smaller to the larger of the two quantities increases.

In the second experiment, Ward and Smuts [56] inquired whether the dogs' performance

could be attributed to immediate perceptual feedback as a result of the simultaneously presented and visually accessible food choices, or whether the dogs had a mental representation of the quantities and could therefore continue to make the correct choice even when the choices were sequentially presented or not visually accessible at the time when dogs made their selection. They tested two dogs and found that the dogs still selected the correct option even when both choices were not visually accessible or presented simultaneously. These findings suggest that dogs, like some non-human primates, can form internal representations of quantity and make mental comparisons of quantity. However, the dogs' performance in experiment 2 was no longer affected by the ratio or numerical distance between the quantities. Therefore, the cognitive mechanism underlying quantity discrimination in dogs is not clear, and further research is needed.

Baker et al. [57] followed up on Ward and Smuts [56] and used the same procedure to investigate quantity discrimination in captive coyotes. The coyotes performed similarly to the dogs, including exhibiting comparable ratio effects, where the performance of the coyotes increased as the numerical distance increased and the ratio between the quantities decreased. Based on this work and a follow-up study examining quantity discrimination in domestic dogs by Baker et al. [58], it appears that domestication did not significantly change quantity discrimination abilities in dogs as compared to coyotes. However, in a study comparing quantity discrimination between wolves and dogs, Range et al. [65] found the opposite result. Although the dogs and wolves tested in this study were raised and housed in identical conditions, dogs performed significantly worse than wolves when asked to select the larger of two quantities of food. In this study, the choices were presented simultaneously but were visually unavailable when the animal made a selection. Thus, it does appear that domestication may have altered quantity discrimination abilities in dogs as compared to wolves. The costs to assessing quantity incorrectly may be very high for wolves in the wild, whereas selection on this ability appears to have been relaxed during domestication of dogs.

Another test of quantity discrimination in the family Canidae focused on hand-raised wolves. In this study, Utrata et al. [60] asked 11 timber wolves to choose the larger number of food items in a

two-way choice task. The wolves were trained on the experimental paradigm and were then presented with one to four food items that were placed sequentially into opaque food containers. To control for other perceptual cues, such as handling time and sound of items being dropped, additional stones were added to the container with the smaller quantity of food items such that there was an equal number of total items placed into each container. Trained wolves were able to choose the larger number of food items, even though the food items were not visible when the wolves made their selection. However, the wolves did not exhibit any increase in performance as the ratio between the quantities decreased. Thus, the performance of the wolves in this study did not follow Weber's law. The wolves in this study behaved similarly to the domestic dogs in the second experiment conducted by Ward and Smuts [56] that we describe above. In both cases, individuals no longer exhibit ratio effects when the food items are not visible at the time of selection. Perhaps dogs and wolves are using a different cognitive mechanism to discriminate between quantities when the final choices are visually available versus when they are unavailable.

It has been suggested that animals may possess two different non-verbal systems for representing numerical values. The first system, called the object-file model [49,66,67], precisely represents small numbers (up to 3 or 4). Each object in a set to be enumerated is represented by a unique symbol. Because the representation of quantity is exact, discrimination of quantities by animals using the object-file model does not follow Weber's law or show ratio effects. The second system, called the approximate number system [64,68,69], approximately represents larger numbers, and possibly small numbers as well. Quantities are represented as continuous mental magnitudes, not precise numbers, and are therefore subject to ratio effects. Discrimination between different quantities using the approximate number system follows Weber's law. Consequently, it is more difficult to discriminate differences between larger quantities and it becomes progressively easier to discriminate quantities as the ratio of the smaller quantity to the larger one decreases. Given that the test subjects in both of these experiments were asked to discriminate between 1-4 objects, these studies suggest that in both dogs and wolves, individuals are potentially using an object-file system to

keep track of a small number of hidden objects but that they rely on an analog-number system when discriminating between quantities that are visually available. Additional study on quantity discrimination in dogs and wolves is necessary to understand whether these species exhibit the expected ratio effects when presented with larger set sizes of objects, especially quantities that are beyond the limits of working memory. It is also interesting that dogs and wolves are behaving similarly in this regard given that domestication appears to have altered quantity discrimination abilities in dogs compared to wolves in the Range et al. [65] study. Clearly, further study is needed in this area to fully understand the effect of domestication, and possibly even captivity, on cognitive abilities such as quantity discrimination.

In a study of spontaneous quantity discrimination in untrained domestic cats, Bánszegi et al. [54] presented cats with three food choice experiments. Cats were able to select the larger quantity of food when both choices were visually accessible and, like dogs, the performance of the cats increased as the ratio between the two choices decreased. However, when the cats were presented with two choices that were then hidden from view, the cats were no longer able to select the larger quantity of food, despite olfactory cues still being available. Thus, it appears that cats are relying on visual cues, such as surface area, when making their decision, and, unlike dogs, are not forming a mental representation of the two quantities. Cats have also been trained to choose between two and three dots in order to obtain a food reward [55]. Cats were able to make this discrimination, however, this study also found that cats appear to be relying on visual information in order to solve this task. These two studies of quantity discrimination in cats have produced conflicting results. In the Pisa and Agrillo [55] study, cats were able to discriminate between 2 vs. 3, whereas in the Bánszegi et al. [54] study, cats failed on this discrimination. Bánszegi et al. [54] suggest that these results may be due to the different methods employed in these studies; specifically, the use of trained versus spontaneous discriminations. Agrillo and Bisazza [70] argue that spontaneous discriminations may be more representative of a species' natural abilities than trained discriminations, which are more likely to demonstrate the absolute abilities of a species.

Similar methods were used to assess the spontaneous quantity discrimination abilities of American sea lions, which are members of the family Otariidae. In a two-alternative, forced-choice task, Abramson et al. [63] presented four captive sea lions with two different options, each consisting of 0 to 6 pieces of fish and asked whether the sea lions could choose the option with more fish. The sea lions were presented with two different experiments. In the first experiment, subjects could see both options at the time of selection, whereas in the second experiment, the fish pieces were dropped into an opaque bucket and were out of sight when the subject made their decision. Sea lions were able to select the larger quantity in the first experiment, when the quantities were presented simultaneously and were visually accessible. Additionally, the performance of the sea lions was affected by the ratio and distance between the two quantities, thus following Weber's law. However, only one sea lion performed above chance in the second experiment. The experimenters were not able to control for potentially confounding perceptual cues in this study, such as surface area in Experiment 1, or dropping duration in Experiment 2. Overall, these results are in line with those of other studies using similar methods to assess spontaneous quantity discrimination abilities in animals. However, further study is needed to determine the extent to which sea lions rely on perceptual cues other than quantity when making their decisions. Additionally, it is not clear why only one individual was able to mentally track the number of fish pieces in the second experiment.

Many of the studies on quantity discrimination have focused on social species, and it is unclear how sociality affects numerical cognition. To address this question, Vonk and Beran [61] presented three trained American black bears with differing numbers of dots on two arrays presented simultaneously on a touchscreen computer. One bear was trained to select the larger number of dots and two bears were trained to select the smaller number of dots. The bears were shown arrays where the number of dots was positively correlated with the surface area that the dots covered (congruent trials), as well as arrays in which the number of dots was negatively correlated with surface area (incongruent trials). The bears performed similarly to non-human primates in both congruent and incongruent trials and were able to preferentially select either the larger or smaller array in both

scenarios. The bears also showed ratio effects consistent with Weber's law. Additionally, one bear was able to select the correct array, even when the dots were moving on the screen. These results demonstrate that the American black bear, a solitary carnivore, is capable of discriminating these quantities, even when presented with moving stimuli. Thus, this ability did not only evolve in social species and is not solely an adaptation stemming from the need to keep track of group members.

Finally, Davis [62] trained a single male raccoon over a six-month period to select a clear cube containing three objects from an array of cubes containing 1, 2, 3, 4, and 5 objects. Alternative stimuli such as olfactory cues, spatial cues, size, and density of the reward were controlled for. The raccoon was able to select three objects when presented with either grapes or metal balls, however, this only occurred after extensive training. The cognitive mechanism that the raccoon used to select three objects is not known, and further study is needed to fully assess the numerical abilities of raccoons. In particular, it would be interesting to determine whether raccoons can exhibit quantity discrimination spontaneously.

As the above studies demonstrate, we are starting to develop an understanding of quantity discrimination abilities among members of the Order Carnivora. Although there is a lot of work left to be done, these studies are beginning to examine quantity discrimination across a number of families within the order, while the multiple studies done on Felids and Canids are giving us a clearer picture of how well developed quantity discrimination is within carnivores. However, all of the above studies were conducted in captivity. Work on captive animals has many benefits, including the ability to gain a high level of control in the presentation of trials and the number of trials each individual experiences. Captive studies also enable researchers to test the cognitive mechanisms underlying quantity discrimination, such as whether carnivores have a mental representation of quantity and how quantities are stored and retrieved in the brain. With captive studies, we can determine the limits of a species' ability to discriminate quantities.

Although in recent years researchers have made a tremendous push to study a greater diversity of species in captivity, as evidenced by the studies on bears, coyotes, sea lions, and

raccoons mentioned above, the field of animal cognition is still severely limited with regard to the number of species that we can study in captivity. Additionally, the largest limitation with captive studies of animal cognition is that we do not know the ecological relevance of the results of these studies for animals in their natural habitat. Just because a sea lion or a black bear can discriminate quantity when they are tested in captivity, does not mean that these species use this ability in the wild, nor does it tell us the extent to which wild animals rely on quantity discrimination to successfully solve problems in their natural habitat. External validity of captive research on animal cognition is especially problematic because the variable of interest, in this case quantity, is rarely the only variable of significance. In the wild, animals do encounter situations, such as territorial disputes, where their ability to discriminate quantity, in this case the number of intruders, could affect their behavior. However, the size, sex, and health of the intruders (or the defender) are additional variables that could greatly influence how an individual would respond in that situation. Other factors, such as the presence of dependent offspring or the proximity to a valuable resource, for example a den or carcass, can also significantly affect an animal's response to intruders, regardless of their ability to discriminate quantity. Thus, it is critical that we compliment the results of these studies on captive animals with studies on wild animals in their natural habitat. Only then can we fully understand which aspects of an animal's environment have been critical drivers of the evolution of numerical abilities.

Relative Numerosity Judgements in the Wild

Game theory predicts that animals should assess the strength and relative numbers of potential opponents before engaging in aggressive interactions [71–73]. In particular, numerical assessment abilities should be well developed in species that experience potentially lethal inter-group conflicts, and where group size can vary dramatically [74–76]. African lions and spotted hyenas are both well armed with sharp teeth and powerful jaws and have potentially lethal intergroup encounters, which

the larger group often wins [77–81]. Additionally, both lions and spotted hyenas live in fission-fusion societies, where members of a social group all defend a communal territory, however, all members of a social group are rarely found together in the same place at the same time, and instead, individuals travel, rest, and forage in subgroups that vary frequently in both their size and composition [79,82–85]. Numerical imbalances may be more extreme in fission–fusion societies than in more cohesive social groups, such as those of some ungulates like the Africa buffalo [86], where members of a social group are typically found together. In fission-fusion societies, it would not be uncommon for a relatively small subgroup from one clan to encounter a relatively large subgroup from a neighboring clan. In these situations, the larger subgroup can attack the smaller subgroup at relatively low cost to themselves. Therefore, the greater variation in subgroup size in fission-fusion societies may lead to higher rates of intergroup aggression. Animals living in fission-fusion societies are likely under increased selection for the ability to assess numerical odds, or the ratio of number of defenders to number of intruders, before engaging in aggressive intergroup interactions.

McComb et al. [14] first introduced playbacks as a novel tool for studying contests between social groups in an investigation of numerical assessment abilities in wild African lions. In this study, we presented female lions with recordings of either one unknown female intruder roaring or three roaring in an overlapping chorus. Female lions were consistently less likely to approach three simulated intruders than one intruder roaring and when they did approach three intruders they approached more cautiously, taking longer to reach the level of the loudspeaker and pausing more frequently on the way to scan ahead and check on the positions of lagging companions. Overall, the number of defending adult female lions, the number of intruders, the number of subadults, and the presence of cubs, all affected approach behavior, with the probability of approach increasing as the number of defending adult females and subadults increased, and decreasing as the number of intruders increased. The best predictor of approach probability was in fact the ratio of number of adult defenders to number of intruders, suggesting that this key information, presented in visual and auditory modalities respectively, was integrated during decision-making. Adult females were also

more likely to approach the intruders when there were cubs present.

Heinsohn [87] conducted a follow-up study where he compared the territorial behavior of lions prides in two locations where the density of lions differs dramatically. Lions in the high-density location approached the calls of simulated intruders faster than lions in the low-density location. Specifically, lions in the high-density location either approached all simulated intruders at the same speed, regardless of numeric odds, or sometimes actually approached playbacks of intruders faster when the odds were low. Thus, it appears that although lions have the ability to assess numerical advantage and respond based on numeric odds, they may choose not to alter their behavior in response to numeric odds in certain environments, such as areas with high competition for resources.

In a key study of numerical assessment in male lions, Grinnell et al. [88] played choruses of single roar bouts of one, two, or three intruder males to groups of one to four resident males. In parallel with what McComb et al. [14] found with female lions, lone adult male lions were also slower to approach the sound source when hearing roars produced by three unknown males within their territory than when hearing roars produced by just one male. Unlike female lions, however, the resident males approached the speaker almost every time. Out of 36 total playbacks, the focal subject failed to approach only three times, and all three of these instances occurred when one male was played roars from three intruders. The latency to approach the speaker for male lions, which is a measure of aggressiveness, was significantly influenced by the number of defending resident males, the number of intruders, and the amount of nearby cover. In contrast to female lions, male approach behavior was not affected by the presence of cubs or subadults. The number of adult females nearby also did not affect approach behavior of male lions.

As the above studies demonstrate, male and female lions both show the ability to discriminate between the playbacks of one and three same-sex conspecifics. This ability can be very advantageous when lions are defending their territory against intruders. However, there are also situations in which lions can benefit from assessing the quantity of opposite-sex conspecifics. Grinnell and McComb [89] considered whether defense by female lions against potentially infanticidal males might also

have contributed to the evolution of quantity discrimination in lions. When new male lions enter a social group, they will often kill the dependent offspring of the resident females. This infanticide is advantageous for the males, as it brings the resident females into estrus an average of 8 months earlier than they would have come into estrus if their cubs survived to independence [90]. However, such infanticide is very costly for the females, as they immediately suffer an enormous direct fitness loss. Adult females will fight to defend their offspring against infanticidal males, and groups of two or more females are more successful at defending their cubs than single females. Thus, it would be beneficial for males to be able to assess the number of opposite-sex conspecifics when they attempt to approach prides of females and to adjust their behavior based on the number of roaring individuals. Grinnell and McComb [89] used playback experiments to test whether extra-pride males are specifically attracted to females (versus males) roaring, and whether these males are more likely to approach a single female roaring alone than a chorus of three females roaring together. As predicted, extra-pride adult male lions avoided the roars of resident male lions, but were attracted to the roars of female lions. Additionally, these male lions were less likely to approach the speaker when the roars of three females were broadcast compared to the roars of a lone female. Thus, it appears that female roaring can attract infanticidal males, males are more attracted to the roars of vulnerable lone females, and females can deter potentially infanticidal males and protect offspring by roaring in groups.

Playback experiments were also used to test the abilities of wild spotted hyenas to assess numerical advantage [15]. Spotted hyenas live in large fission-fusion social groups called clans, which contain up to 90 individuals that cooperate to defend a group territory [82–85]. Given the similarities between the fission-fusion societies of spotted hyenas and African lions, we predicted that spotted hyenas should show comparable numerical assessment abilities to those seen in lions. Specifically, we predicted that spotted hyenas should be more aggressive and more willing to approach the calls of unknown intruders when they had the numerical advantage, and they should be more vigilant and less willing to approach the speaker when they were outnumbered. We tested these

predictions by presenting hyenas in two study clans in the Masai Mara National Reserve in Kenya with long-distance contact calls, known as whoops, produced by one, two, or three unknown hyenas, or 'intruders'. We used calls from one, two, or three unknown hyenas to determine whether hyenas simply make the distinction between one versus many intruders, or whether they are able to discriminate and keep track of specific numbers of intruders. To avoid confounding stimulus intensity with stimulus number, in this study we presented the hyenas with calls played sequentially instead of playing calls from multiple intruders in an overlapping chorus. To control for stimulus duration, we played each focal hyena three consecutive whoop bouts, varying the identities of the callers but not the number of whoop bouts heard. When presenting the focal hyena with calls from one intruder, we repeated a whoop bout produced by one individual three times. For two-intruder playbacks, we began with a whoop bout produced by one individual, followed by a whoop bout produced by a different individual, followed by a whoop bout produced by either the first or second individual. For three-intruder playbacks, we presented whoop bouts produced by three different individuals. Thus, crucially, hyenas in each treatment heard the same number of whoops over the same period of time, with the only difference between treatments being the number of different individuals vocalizing.

Our use of consecutive and non-overlapping calls as sound stimuli required hyenas to distinguish among individuals based on their vocalizations in order to determine the number of unique callers. In addition, because the stimulus calls were not played simultaneously, focal hyenas had to remember which individual they had heard earlier to identify new individuals. If hyenas simply count calls without discriminating between callers, then they should respond similarly to all three playback treatments. However, this was not the case. Hyenas conformed to predictions of game theory by increasing vigilance to playbacks of multiple unfamiliar intruders. Furthermore, they distinguished not just between calls produced by one versus multiple intruders, but kept track of the specific number of intruders. Hyenas responded with increasing levels of vigilance to calls produced by one, two and three unknown intruders. They were also more willing to take risks and were more

aggressive in approaching the speaker when they outnumbered calling intruders. Specifically, hyenas appeared to respond based on numeric odds, or the ratio of defenders to intruders. Thus, hyenas not only kept track of the number of intruders, but they also calculated the number of individuals present in their own group. Hyenas then were able to compare those group sizes and respond appropriately.

Although hyenas did respond to the playbacks based on numerical advantage, we also found consistent differences among individuals in how vigilant they were across all three treatment conditions. These differences could not be attributed to factors such as social rank, but instead appear to be more akin to differences based on personality. Consistent individual differences were also found in a playback study of cooperation in territory defense in African lions [91]. In this study, Heinsohn and Packer [91] played the calls of territorial intruders to groups of female lions and found that some females consistently approached the speaker first, while other females consistently lagged behind. A minority of lagging females adjusted their behavior depending on the numeric odds and joined their group mates when the ratio of defenders to intruders decreased and their participation was most critical. However, the same number of females showed the opposite pattern, and the majority of females showed no change in their lagging behavior as the numeric odds decreased. These differences in approach behavior could not be attributed to differences in fighting ability, such as age or body size. Thus, as in the hyenas, it appears that lions may also exhibit individual differences in their response to playback experiments due to differences in the personalities of the study subjects. Moreover, in both species, there is considerable evidence that these wild carnivores that live in fission-fusion societies are able to assess numerical advantage and respond appropriately based on numeric odds.

There have also been several playback experiments investigating numerical cognition in wild canids. Harrington and Mech [92] investigated howling in wolves and its function in territorial maintenance and found that wolves in larger packs howl in response to human howls more often than wolves in smaller packs. Using long-term behavioral observation data on packs of wolves in Yellowstone National Park, Cassidy et al. [93] found that relative pack size was a key determinant of

the probability that each wolf would chase members of a rival pack. The wolves were more likely to chase rival packs where they outnumbered their opponents and wolves appeared to be able to assess numerical advantage rapidly during inter-pack encounters. Relative pack size was also found to improve the probability of a wolf pack displacing their rivals [94]. However, packs that contained greater numbers of adult males or older members also experienced a greater probability of winning interpack interactions, even when they were outnumbered. Thus, although numerical advantage is a critical variable determining the outcome of aggressive interactions between packs of wolves, group composition is also an important factor. Wolves therefore must rapidly assess not only their relative group size, but also the age and sex makeup of rival groups compared to the composition of their own pack when deciding whether or not to approach a rival group.

These playback experiments on African lions, spotted hyenas, and wolves demonstrate that social carnivores have evolved the ability to assess numerical advantage and rapidly decide whether or not to engage in a potential conflict with territorial intruders based on numeric odds. However, we do not yet know how African lions, spotted hyenas, and wolves mentally represent quantity. Although there is evidence from captive studies of carnivores to support both non-verbal systems, the object-file and analog-number systems [56,57,60,63,64,95], the cognitive mechanisms underlying numerical assessment abilities have rarely been considered in studies of wild animals.

Bonnani et al. [96] assessed the potential for both non-verbal systems of numerical representation in a study of intergroup conflicts in free ranging dogs. Using behavioral observations of intergroup interactions between packs of free ranging dogs that varied in size, Bonnani et al. [96] found evidence that relative group size was a key predictor of the probability that at least one member of a focal pack would aggressively approach an opposing pack. Bonnani et al. [96] also found support for both systems of numerical representation in dogs. Relative group size impacted approach behavior for members of both large and small packs, which supports the approximate number system. Additionally, dogs aggressively approached opposing packs equally often—regardless of the numeric odds—when both packs contained four or fewer individuals, which

supports the object-file system. Thus, dogs may be capable of using both systems, depending on the context.

The use of playback experiments to assess quantitative abilities of animals in their natural habitats is not limited to carnivores. There have been a number of studies demonstrating numerical assessment abilities through the use of playback experiments and observational data in non-human primates, such as chimpanzees [16,97,98] and howler monkeys [17,45]. In birds, playback experiments have also been used to show that nestling barn owls assess the number of competing siblings when begging for food from their parents [99] and that groups of a cooperatively breeding subdesert mesite were less likely to approach, but vocalized more, as the number of simulated intruders increased [100]. Groups with a higher ratio of adult males to adult females were also more likely to approach the playbacks, and the likelihood of a group approaching increased when the ratio between the number of focal adult males and the number of intruder adult males increased.

As the above studies show, playback experiments offer a window into how social animals perceive the world and have now been used effectively across a diversity of taxa. Such experiments are a powerful tool for investigating many aspects of social and numerical cognition and the work described here convincingly demonstrates that a range of carnivore species tested in their natural habitat show impressive abilities to discriminate quantity and assess numerical advantage. These playback experiments provide evidence that the advantage of minimizing or avoiding the costs of fighting against a larger group of conspecifics may be a possible selective pressure leading to the evolution of numerical assessment abilities in social species [14].

Despite their effectiveness, playback experiments do have some limitations that should be considered when designing these studies and when interpreting the results of experiments that use this methodology. First, we have to be cautious when designing playback experiments to ensure that the stimuli we are using to elicit a response do not have an unknown meaning. For example, chimpanzees distinguish between scream calls given in different contexts. Screams given when the vocalizer was the recipient of mild as opposed to severe aggression elicited different responses, as

did acoustically similar screams given when an individual experienced social frustration but no physical violence [101]. Thus, calls that sound the same to us can have very different meanings to our study animals and elicit very different responses that are unrelated to numerical advantage.

Second, the location of a playback experiment can greatly alter the responses exhibited by the focal animal. If a focal animal hears the call of a potential territorial intruder near the border of its territory, it may respond less aggressively than if it hears the same call in the center of its territory [[102–104]; but see [16,94,105]]. Likewise, the call of a competitor may elicit a much more aggressive response when played near a valuable resource, such as a carcass or a den [92]. The importance of location for determining the outcome of intergroup interactions is well illustrated in a study of capuchin monkeys [106]. Although relative group size was an important determinant of success in intergroup contests, with each additional group member increasing the odds of winning by 10%, location was also critically important. In capuchins, small groups can defeat much larger groups when they are in the center of their home range, and the odds of a group winning an intergroup contest decreases by 31% for each 100m that it moves away from the center of its home range.

Third, social influences, such as the presence of dependent offspring can also change the response of focal animals to playback experiments, as was the case in our original study of African lions [14]. Here we found that when cubs were present, female lions always approached the speaker, regardless of the numeric odds they were facing. However, when no cubs were present, female lions responded based on numeric odds. Without cubs, lionesses almost never approached the speaker when they were outnumbered, and they only began to approach the speaker more frequently once they significantly outnumbered their opponents. Examples of other social influences that can affect the response of a focal animal to a stimulus presented during a playback experiment include the personality and social rank of nearby group members, as well as the strength of the relationship between the focal animal and nearby conspecifics. For example, playbacks of female distress calls in chacma and olive baboons elicited a stronger response in some males than others [107,108]. Males that exhibited close affiliative bonds, or ‘friendships’ with females (characterized by high rates of

allo-grooming and infant handling and low rates of agonism) responded more strongly (measured as visual orientation and movement toward the speaker) to playbacks of their female ‘friend’ in distress than did control males.

Fourth, as evidenced by our research on spotted hyenas, there is substantial individual variation in responsiveness to playbacks, with some individuals being consistently more vigilant in response to simulated calls of territorial intruders while others are consistently less vigilant, regardless of the number of individuals calling [15]. Individual personality has also been shown to influence the response of territorial male great tits to recordings of simulated intruders [109]. Males with lower exploration scores were less likely to approach the source of the sound than males with high exploration scores and sang more songs that were shorter and contained slower element rates than the songs of more exploratory males. Additionally, the response of the males to the playback was influenced by the personality of their neighbor, showing again that social factors other than numerosity can influence the response of animals to these playback experiments.

In addition to personality, individual traits such as body size, age, sex, dominance status, and motivation can all potentially affect the response of animals to playback experiments. Vocalizations encode information about the physical characteristics of the caller, including body size, age, and sex [110–115]. Large, medium, and small domestic dogs were presented with growls mimicking dogs that were either 30% larger or 30% smaller than the focal individual [110]. The response of the dogs depended on both their own size and the size of the growling dog. Large dogs consistently responded differently to growls coming from smaller versus larger dogs and showed more interest in investigating non-aggressively the playbacks of dogs smaller than themselves than they did in the playbacks of dogs larger than themselves. In contrast, small dogs did not respond differently to playbacks of smaller versus larger dogs, and showed less interest overall in investigating the playbacks of both sizes than did the medium and large dogs. Vocalizations also can encode information about the emotional arousal of the caller and this can affect the motivation of the listener to respond. The whoop call of the spotted hyena is a loud vocalization that contains multiple calls, or

whoops, separated by silent pauses, or inter-whoop intervals. Spotted hyenas can vary the duration of these inter-whoop intervals, resulting in faster or slower calls. Theis et al. [116] found that the inter-whoop interval encodes information about the current emotional state of the caller and that hyenas respond to this information. Whoop bouts emitted by juveniles during periods of social excitement have shorter inter-whoop intervals, and conspecifics are significantly more likely to respond to these whoop bouts by approaching the caller.

Thus there are many factors in addition to the variable of interest that can influence the behavior of focal animals in playback experiments. Most of these factors can be controlled for by careful consideration of the vocalizations used as sound stimuli and by ensuring a large sample size of focal animals to account for consistent individual differences in behavior as well as different responses based on age, sex, body size, or motivation of the listeners. Researchers must also counterbalance the presentation of sound stimuli and ideally use a number of different recordings as stimuli to avoid biased responses based on a particular characteristic of one recording, such as a vocalization that was emitted during a period of social excitement. However, in addition to carefully designing experiments to control for these factors, we can also include these variables in our experimental design in order to assess their relative importance.

Cross Modal Individual Recognition in Carnivores

As Benson-Amram et al. [15] showed, the ability to discriminate between, and even recognize, individual conspecifics is a critical skill that wild animals must possess in order to then be able to discriminate the number of calling conspecifics and respond precisely based on numerical advantage. However, individual recognition has rarely been considered in studies of quantity discrimination and the extent to which carnivores are able to individually recognize conspecifics has been left largely unexplored. In order to truly demonstrate individual recognition, it is necessary to show that a test subject identifies a specific individual and that there is a match between current individually distinct

cues, such as the individual's vocalization, and information about that individual that is stored in the memory of the test subject, such as the individual's last known location [117].

Historically, it has been very difficult to obtain evidence of individual recognition, as opposed to the less restrictive category of individual discrimination, where an individual demonstrates that it distinguishes between unique individuals, without necessarily recognizing each specific individual. Recently, studies of cross-modal processing have provided some of the most convincing evidence for individual recognition in multiple species in captivity. Cross-modal processing is the ability to integrate information from multiple senses and was first demonstrated between animals in the domestic horse [118]. In this study, horses watched a familiar herd-mate disappearing behind a barrier before the contact call of that particular individual or of another familiar herd-mate were played from the point of disappearance. If there was a mismatch between the cues, which occurred when the vocal and visual cues were from two different individuals, horses responded much more strongly than when the cues were taken from the same individual. In addition to domestic horses, there is now direct evidence for cross-modal recognition in crows, rhesus monkeys, and domestic dogs, all of which have been tested in captive or domestic settings [119–121]. In the study of domestic dogs, Adachi et al. [119] even demonstrated cross-modal matching between the dog owner's voice and the owner's face. Specifically, dogs looked longer when the face shown to them on an LCD screen did not match the voice that was being played back to them versus when the face and voice both came from the owner. Horses can also correctly match visual and vocal cues when faced with two familiar human handlers [122].

Until recently, cross-modal recognition had not been directly shown in the wild during natural social communication among conspecifics. However, we have now demonstrated this ability in wild African lions, a species where true individual recognition might be expected given the repeated interactions and long-term social relationships that exist in this species, and their frequent use of visual, olfactory, and vocal signals in communication [123]. As in other studies of cross-modal recognition, we investigated individual recognition in wild lions using an 'expectancy violation'

paradigm, but here a vehicle was used to create a visual block between our test subject and another member of their social group. After a pause of 30 seconds to 1 minute, which was done to ensure that the test subject had to retrieve some information about the identity of the blocked individual from memory, we played a roar from behind the vehicle that either matched the identity of the blocked individual (a congruent trial) or was recorded from a different group member (an incongruent trial). If lions individually recognized members of their social group, then they should have exhibited a stronger response to incongruent trials. As predicted, we found that both male and female lions responded to incongruent trials by spending a greater proportion of time after the playback moving and looking in the direction of the simulated call than they did after congruent trials. Following the incongruent playbacks, lions also initiated a higher rate of allo-rubbing, which could be a displacement behavior indicative of social stress [124]. These results are consistent with lions recognizing the auditory-visual mismatch and being capable of cross-modal individual recognition.

Although work on individual recognition in wild carnivores is in its infancy, it appears that wild carnivores, at least those living in complex societies such as the fission-fusion societies found in lions and spotted hyenas, likely possess the ability to recognize individual group members and to discriminate between group members and unfamiliar conspecifics [15,123]. Additionally, our work on wild spotted hyenas shows that these animals not only categorize vocalizations from conspecifics as known versus unknown, but actually discriminate between unknown individuals and recognize when a call is coming from the same unknown individual or a different one, even when these calls are played minutes apart [15]. Individual recognition is a fundamental cognitive ability, and is a critical building block for many complex social behaviors. Our playback experiments have now shown that individual recognition is a critical component of numerical assessment abilities in social contexts, when animals are using numerical skills to count conspecifics and assess numerical advantage. Interestingly, the process of assessing the number of individuals in a co-operative or competitive situation must incorporate, at some level, a sense of what one individual constitutes. Our work collectively points to carnivores having cognitively rich multi-modal representations for

different individuals. Perhaps if ‘the individual’ is an evolutionarily ancient concept [117], this integrated perception could also provide a key baseline for numerical abilities in social species – the concept of ‘one’.

Conclusions and Future Directions

Decades of research on numerical cognition in both captive and wild carnivores has brought forth convincing evidence that many carnivore species have advanced abilities to discriminate between quantities and to assess numerical advantage. Work on captive carnivores shows that multiple species from across the order Carnivora demonstrate comparable quantity discrimination abilities to those seen in primates. Although many carnivores do show a preference for making a decision based on other perceptual cues such as surface area, they are often able to correctly identify a larger quantity when those other perceptual cues are controlled for. Additionally, as seen in primates, most carnivore species that have been tested in captivity do exhibit ratio effects consistent with Weber’s Law, indicating that numerical abilities are a foundational cognitive ability that are widespread throughout the animal kingdom and that the evolution of numerical abilities has deep phylogenetic roots.

Future work on numerical abilities in carnivores should focus on investigating the differences in numerical abilities among an even more diverse set of species, particularly species that differ in their social and ecological environments. For example, further study is needed to understand if animals living in complex societies exhibit different numerical abilities from solitary animals. Further work is also needed to investigate whether diet and hunting strategy have influenced the evolution of numerical abilities, as work comparing captive wolves and dogs would seem to suggest. It would be very beneficial to conduct comparative studies testing numerical abilities in obligate carnivores, omnivores, insectivores, and herbivores, as well as comparing the numerical assessment abilities of predator species that hunt cooperatively to solitary predators and prey species.

Despite the recent advances in understanding numerical assessment abilities in wild carnivores, many questions remain unanswered. The playbacks conducted to date have not yet identified the cognitive mechanisms used by social carnivores to assess numerical advantage. Benson-Amram et al. [15] did show that hyenas were able to keep track of the number of vocalizing intruders, even though the calls were played sequentially and not in an overlapping chorus. This demonstrates that the hyenas have some ability to mentally keep track of quantity and are not simply responding based on immediate perceptual feedback. However, we do not yet know whether wild carnivores use an analog magnitude system to represent quantities, which would be expressed as ratio-dependent responses following Weber's law, or whether they use an object-file system to represent small numbers of objects, which would be expressed by demonstrating a lack of ratio effects when tracking and discriminating between small quantities [19]. The vast majority of studies in wild carnivores have presented only a small number of objects to the study subjects, and the one study that has investigated the numerical systems used by a wild carnivore found some evidence for both systems. We are particularly interested in understanding whether the numerical assessment abilities that we have seen in playback studies persist when wild animals are presented with larger group sizes. For example, would hyenas be able to respond based on small differences in numerical advantage even when confronted with larger numbers of intruders? Currently, we do not know at what point this ability breaks down. These results could be extremely informative in understanding the cognitive mechanisms behind quantity representation in carnivores. It would also be interesting to study in more detail, across a wider range of species, the degree to which numerical advantage predicts outcomes of disputes over valuable resources, such as territory or competition for access to a carcass.

It is not always clear how to take the methodological advances from studies in captivity and apply them to addressing the same questions in studies of wild animals. We are currently working on an experimental set-up that will enable us to implement methods from captive work on primates [125–129] and bears [61] to test numerical abilities in a variety of carnivores in the field.

Specifically, we are developing automated testing pods that will present images to participating animals on a touchscreen computer. Puzzle feeders will be housed inside testing pods with room for only one individual to enter and participate in experiments. Our testing pods will first distinguish individual animals using Radio Frequency Identification (RFID) and then administer one of several cognitive tests according to the animal's experimental group and training stage. With these data, we will be able to ask whether results from studies of numerical cognition in carnivores in captivity accurately reflect the performance of these same carnivore species when tested in their natural habitats.

Previous research comparing innovative problem solving between wild and captive spotted hyenas found that the captive animals greatly outperformed their wild counterparts [130]. We were able to rule out hypotheses suggesting that these differences result from excess energy or time available to captive animals. Instead, it appears that the significant difference in problem-solving success between the wild and captive populations was largely due to differences in exploration and neophobia. The captive hyenas had fewer distractions and fewer conflicting motivations than did the wild hyenas, which probably led to more focused and higher-quality work time for the captive individuals. Additionally, the captive hyenas had more experience with, and exposure to, man-made objects and therefore were less neophobic and more innovative than the wild hyenas. It is not clear whether this difference in performance between captive and wild animals that were presented with the same problem is unique to the type of challenge the hyenas were facing in these experiments, an innovative problem-solving task, or whether we would also see this same difference in performance between captive and wild populations on other cognitive challenges, such as tests of quantity discrimination. We suspect that the captive and wild populations will still demonstrate differences in neophobia and exploration when facing other cognitive tasks, however, neophobia and exploration may not affect success on these other cognitive tasks to the same degree that they influenced success on a novel technical problem.

Differences in performance on cognitive challenges between wild and captive individuals

may also be due to a possible ‘enculturation effect’, whereby captive animals develop more human-like cognitive capacities due to their interaction with humans and their experience with man-made objects [131–133]. Additionally, captive animals may also perform better in cognition experiments because they may have learned the affordances of manmade objects better than wild animals and therefore may be more adept at manipulating these objects in novel situations [134]. For example, one can imagine that the extensive training and cumulative experience that many captive animals acquire when they are the subjects of multiple different experiments to assess their cognitive abilities could increase the performance of these animals on novel cognitive challenges, simply because they are used to being tested and are habituated to the experience of manipulating objects or touch screens for a food reward. If we find that captive animals routinely outperform their wild counterparts on cognitive challenges, then we will have to be very careful in our interpretation of our results from these studies.

Although our investigations of numerical cognition in carnivores are just beginning, the studies described here show that both captive and wild carnivores demonstrate impressive abilities to discriminate between different quantities and to make quick calculations of numeric odds. Because carnivores can be difficult to test in captivity, they have often been overlooked in studies of animal cognition. As we discuss here, playback experiments have proven to be a powerful tool for investigating the numerical cognitive abilities of several carnivore species in the wild while also enhancing our understanding of the factors that animals consider when solving quantitative problems in their natural habitats. Additionally, playback experiments have also been used to test for other cognitive abilities, such as individual discrimination and cross-modal recognition, which can play a critical role in the ability of animals to assess numerical advantage. Recent technological advances are now making it possible to bring traditional laboratory studies into the field as well. Combined, data from these experiments will continue to inform our understanding of numerical assessment abilities in wild carnivores, as well as in other taxa. These experiments enable us to assess the relative importance that wild individuals in a diverse array of species place on quantitative information when

faced with complex decisions. Additionally, these experiments provide critical data that clarify the evolution of numerical abilities.

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Ethics

All ethical approvals for the work we have reviewed here can be found in the original articles. The hyena research reviewed here was described in Animal Research Application No. 07/08-099-00, approved most recently on 29 April 2014 by the Institutional Animal Care and Use Committee of Michigan State University.

Data Accessibility

The datasets supporting this review article are associated with the original articles that we reference.

Authors' Contributions

SB-A, GG, and KM all conducted fieldwork described here and drafted the manuscript. All authors gave final approval of the version to be published.

Competing Interests

We have no competing interests.

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